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FLORIDA SCRUB-JAY DEMOGRAPHY IN DIFFERENT LANDSCAPES

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Florida Scrub-Jay (*Aphelocoma coerulescens*) demography and cooperative breeding from 1988 to 1993 at two sites (HC and T4) on John F. Kennedy Space Center's Atlantic coast. The results from HC and T4 sites were compared with results from the Archbold Biological Station in central Florida. The T4 population showed evidence of reproductive success and immigration, resulting in a nearly equal nonbreeder to breeder ratio. Nearly all young Florida Scrub-Jays delayed breeding for at least two years at T4, similar to Archbold. The HC population decreased because of poor survival, and the nonbreeder sex ratio was biased towards males. During the first year after hatching, nearly one of every five HC females bred. Pairs with nonbreeders (usually had greater reproductive success than pairs without nonbreeders) at HC and Archbold, but not T4. Pairs with nonbreeders usually had greater reproductive success than pairs without nonbreeders at Archbold, but not at HC or T4. Female breeder mortality was slightly higher than male breeder mortality at T4 and HC, but not at Archbold. We concluded that predation contributed to differences in demographic patterns between sites. Received 3 July 1995, accepted 21 September 1995.

Florida Scrub-Jay (*Aphelocoma coerulescens*) is a bird from oak-dominated scrub on the Atlantic coast of Florida (Archbold), where the land is excessively drained, contains few trees, and has few trees (Fitzpatrick 1984, 1991). One of the major populations of the Florida Scrub-Jay occurs on the John F. Kennedy Space Center (KSC; Cox 1987). The KSC habitat is composed of patches of xeric, poorly drained flatwoods and marshes (Breininger et al. 1995) and is a result of alterations of the natural KSC habitat. The KSC habitat has taller trees and more openings than optimal scrub (Breininger 1981; Breininger and Hinkle 1992a,

the KSC habitat is a permanent all-purpose territory surrounded by a permanently flooded area (Breininger et al. 1995). Except for loss and fragmentation, the KSC habitat disperses short distances (usually within 100 m widths) and occupy a small area. Young remain as nonbreeders with the breeders for at

least one year, participating in predator detection, territory defense, and care of offspring (Woelfenden and Fitzpatrick 1984). Florida Scrub-Jay mortality is nearly always caused by predation (Woelfenden and Fitzpatrick 1984, 1991). They have a highly coordinated sentinel system that is important for detecting hawks, which are rare during the season of highest breeder mortality at Archbold (McGowan and Woelfenden 1989). Hawks are especially common at KSC during migration because the Atlantic coast is a hawk migration route (Heintzelman 1986).

Here, we compare reproductive success, survival, family sizes, immigration, and emigration at two KSC study sites. We also compare cooperative breeding features using: (1) the nonbreeder distribution among territories; (2) the proportion of jays remaining as nonbreeders for four years after hatching; (3) nonbreeder effects on survival and reproductive success; and (4) pair-bond fidelity. These features and the seasonality of mortality are compared with findings at Archbold (Woelfenden and Fitzpatrick 1984).

METHODS

Study sites.—KSC is a 57,000-ha barrier island; elevations range from sea level to 3 m. Scrubby flatwoods and scrub are the main upland communities,

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being dominated by scrub oaks (*Quercus geminata* and *Q. myrtifolia*) on well-drained soils and saw palmetto (*Serenoa repens*) and mesic shrubs (e.g. *Lyonia lucida*, *Ilex glabra*) on poorly drained soils (Schmalzer and Hinkle 1992a, b). Scrubby flatwoods differ from scrub by having a sparse slash pine (*Pinus elliotii*) canopy. Sand pines (*Pinus clausa*) are rare. Flatwoods and scrub plants and animals are adapted to periodic fire, and composition is altered little by burning (Abrahamson 1984, Breininger and Schmalzer 1990, Breininger and Smith 1992, Schmalzer and Hinkle 1992a, Breininger et al. 1994).

Two study sites, 12 km apart, were selected in Florida Scrub-Jay population centers on KSC (Breininger et al. 1991). The T4 site was in scrubby flatwoods, and the HC site was within scrub. The HC site was subjected to 20 years of fire suppression before 1979, as was most of KSC. Photographic sequences (1943–1979) showed that natural openings disappeared from HC, and the landscape became increasingly forested (interlocking canopies of trees taller than 5 m). The T4 site was burned by at least one wildfire during the fire suppression period and did not lose openings among scrub oaks, although forests developed in several areas formerly used for agriculture. Forests at T4 were dominated by slash pines. Forests at HC were dominated by *Quercus virginiana*, *Q. laurifolia*, *Sabal palmetto*, *Persea borbonia*, *Acer rubrum*, and *Salix caroliniana*. Both study areas burned five times since 1979. Prescribed burns at T4 were effective at keeping shrubs from exceeding optimal height and maintaining openings among scrub oaks (Duncan et al. 1995). The T4 study site was adjacent to private lands where scrub has undergone habitat destruction and fire exclusion. Prescribed burns at HC have not effectively reduced shrub height in many areas, and natural openings have not returned (Schmalzer and Hinkle 1992a). The HC and T4 sites differ from Archbold by having a shallower water table, more saw palmetto, greater nutrient availability, and no *Quercus inopina* or *Sabal etonia* (Abrahamson 1984, Schmalzer and Hinkle 1992b).

Field procedures.—Color-banding, territory mapping, and most demographic studies (field and data analyses) followed procedures described by Woolfenden and Fitzpatrick (1984). Nearly all resident Florida Scrub-Jays were banded during the first few months of our study. Nestlings were banded on day 11 after hatching, and immigrants were banded within several months of their arrival. Breeders, nonbreeders, and sexes were distinguished using behavioral attributes described by Woolfenden and Fitzpatrick (1984). Nests were visited at least once a week. All Florida Scrub-Jays present were confirmed during the last week of each month. Peripheral surveys were conducted to locate individuals that dispersed up to three territory widths beyond the study area.

Data analyses.—The study was conducted from 1988 to 1993. By definition, each study year began on 1 April and ended on 31 March. Fledglings were esti-

mated as the number of young counted in or near the nest around day 17 after hatching. Nestlings and fledglings were aged using descriptions by Woolfenden (1978). Juveniles were defined as young present in July, when most jays approached nutritional independence (Woolfenden and Fitzpatrick 1984). For each year, the number of fledglings, juveniles, and yearlings produced per breeding pair was calculated. Survival (no. of survivors/no. alive during beginning of study year) was calculated for the periods: (1) fledgling to juvenile, (2) fledgling to yearling, (3) juvenile to yearling, (4) yearling to two-year-old, and (5) annually for older nonbreeders.

Differences in annual production of fledglings, juveniles, and yearlings were tested using Mann-Whitney *U*-tests (SPSS Inc. 1994). Comparisons of breeder survival were tested using log-likelihood ratio tests (SPSS Inc. 1994). Because of low sample sizes, comparisons of fledgling survival for pairs at T4 and HC were tested using log-likelihood tests by combining data from all years. Differences in annual family sizes and in annual fledgling production between pairs with and without nonbreeders were tested using Mann-Whitney *U*-tests. Fledglings, juveniles, and yearlings produced by experienced pairs with and without nonbreeders were combined from all years because of low sample sizes. Differences in fledgling, juvenile, and yearling production between experienced pairs with and without nonbreeders were tested using Mann-Whitney *U*-tests. Combining data across years violated assumptions of independence because experienced pairs involved many of the same individuals, although the same pairs often were not consistently with or without nonbreeders. The log-likelihood test was used to compare fledgling with juvenile survival and juvenile with yearling survival for experienced pairs with and without nonbreeders by combining data for all years. Mean fledgling production for pairs having at least one novice breeder was calculated after combining data from all years. The log-likelihood test was used to compare annual breeder survival among pairs with and without nonbreeders and annual male and female breeder survival.

Data on the number of nonbreeders within families were combined for all years to quantify the proportion of families within each of seven family size classes (i.e. zero to six nonbreeders). All Florida Scrub-Jays having a known history since hatching were combined within each study area. These data were used to quantify how many males and females delayed breeding for each of the first four nesting seasons after hatching. The continuity of pair bonds between successive breeding seasons was compiled for all years. Pair-bond attributes between breeding seasons were assigned to one of five categories: (1) both breeders remained paired together; (2) one breeder paired with a replacement breeder after the death of its spouse; (3) mortality of both breeders; (4) one breeder became a nonbreeder after loss of its territory

of Florida Scrub-Jay demography at John F. Kennedy Space Center and Archbold
ues are means.*

	Kennedy Space Center		Archbold (1969-1986)	
	T4 site 1989-1993	HC site 1988-1993	Periodically burned	Unburned
	1.83	1.11	1.97 ^a	1.58 ^a
	0.96	0.47	1.23 ^a	0.80 ^a
	0.62	0.32	0.68 ^a	0.36 ^a
	0.76	0.80	0.79 ^a	0.72 ^a
	0.34	0.29	0.31 ^a	0.23 ^a
t survival	0.72 ^a	0.73 ^a	0.74 ^a	No data
	3.15	2.78	3.00 ^a	No data

calculate means.

Fitzpatrick (1991).

Fitzpatrick (1984).

a few nonbreeders may have become breeders beyond peripheral surveys.

its spouse; and (5) divorce.
s for male breeders, female
were quantified by summing
month for all years and then
totals by the total number of

RESULTS

duction (1988 to 1993) was
T4 (Table 1), although dif-
ferent only in 1990 ($P < 0.001$).
Mean juvenile production
at T4, although HC had
reduction only in 1989 (P
 < 0.001). Mean yearling
at HC than T4, although
between HC and T4 were
 > 0.05). Mean breeder and
are similar at HC and T4,
ratios never differed sig-
nificantly for HC and T4. Mean fam-
ily size was significantly lower than T4
(0.3).

territories within the T4 study
area (14 (1990), 16 (1991), 15
(1992), and 18 (1993)).
Increases in territory den-
sity occurred except for
the period between 1989 and
1990. Budding occurred
when a male attracted a female from
an established territory in which he was
lone and Fitzpatrick
territories increased at HC
expansions, although ter-
ritory size was not in-
creased. The numbers of ter-
ritories in the original HC study area were

21 (1988), 22 (1989), 18 (1990), 18 (1991), 18
(1992), and 18 (1993). The numbers of territories
studied were 21 (1988), 23 (1989), 21 (1990), 22
(1991), 33 (1992), and 31 (1993) due to study-
site expansions.

Jay populations increased at T4 but decreased
at HC. Twenty breeder females died and 20
yearling females were produced at T4. Fifteen
breeder males died, but 24 yearling males were
produced at T4. Forty breeder females died, but
only 23 yearling females were produced at HC.
Twenty-five breeder males died and 26 yearling
males were produced at HC. Twenty-one fe-
males immigrated into T4 and only two females
emigrated from T4. Seven males immigrated into
T4 and four males emigrated. Seventeen fe-
males immigrated into the HC study area and
only four females emigrated. Eight males im-
migrated into HC and four males emigrated.
No emigrant was less than one year old or was
a breeder at the time of emigration. A few jays
may have emigrated beyond our detection. Only
2% of the HC immigrants became nonbreeders,
whereas 32% of the T4 immigrants became non-
breeders. Other immigrants became breeders.
Male nonbreeders exceeded female nonbreed-
ers when mean family sizes were less than 3.0,
but female nonbreeders exceeded male non-
breeders when mean family sizes exceeded 3.0
at T4 (Fig. 1). There were always more male than
female nonbreeders at HC. More pairs had non-
breeders at T4 than at HC.

Pairs with nonbreeders did not have higher
fledgling production than pairs without non-
breeders at T4 (Table 2). Pairs with nonbreeders
had higher fledgling production than pairs
without nonbreeders at HC, although annual
differences were significant for only two of six

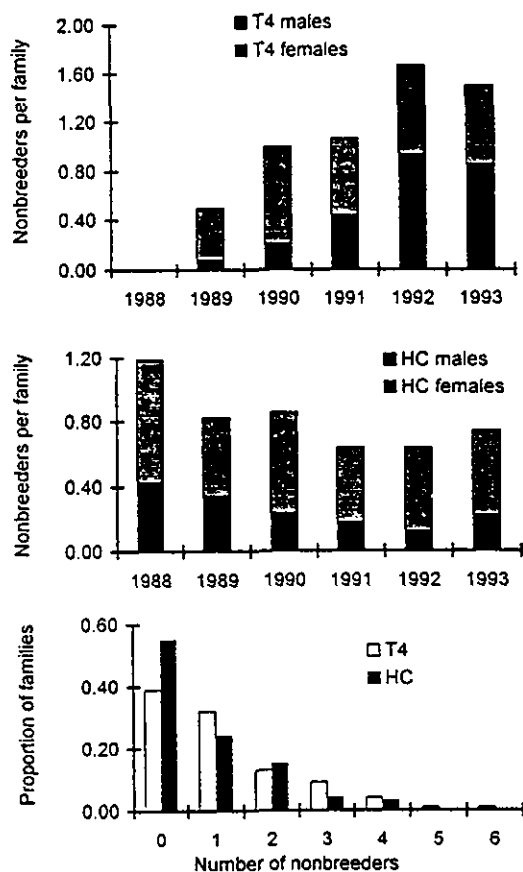


FIG. 1. Mean number of male and female nonbreeders per family of Florida Scrub-Jays and distribution of nonbreeders among territories at two sites on John F. Kennedy Space Center.

years. At HC, experienced pairs with nonbreeders had higher reproductive success than experienced breeders without nonbreeders (Table 3). Experienced pairs with nonbreeders had

higher fledgling survival to the juvenile stage, but not higher juvenile-to-yearling survival than experienced pairs without nonbreeders at T4 and HC. The mean number of fledglings/pair was 0.38 at HC ($n = 8$) and 1.86 at T4 ($n = 13$) for pairs containing at least one novice breeder. At HC, reproductive success was unusually poor in 1990, when only one family produced juveniles.

Survival of breeders in pairs with nonbreeders was not consistently higher than survival in pairs without nonbreeders at T4 or HC (Table 4). Sex differences in survival seldom were significant, yet male breeders had higher survival than female breeders in all six years at HC (Table 5). At T4, male breeders had higher survival than female breeders in three of five years, and the sexes had equal survival during two years. At HC, breeder survival was about average in 1990, even though reproductive success was especially poor.

Mortality was lowest in December and January and highest during March, September, and October (Fig. 2). Breeder survival was also low in July. Breeder female mortality was high during nesting (April and May). Breeder mortality was the major cause of pair-bond disruption, and, in most cases, a lost breeder was soon replaced by a new individual (Fig. 3). Most young delayed breeding for at least one year after hatching but rarely for more than three years; more than half of them became breeders within two years after hatching (Table 6).

DISCUSSION

Demographic success (male yearling production exceeding male breeder mortality) and immigration by many females caused the popu-

TABLE 2. Florida Scrub-Jay fledgling production (fledglings/pair; \bar{x} , with n in parentheses) for pairs with and without nonbreeders at John F. Kennedy Space Center, Florida.*

Year	T4 site		HC site	
	With nonbreeders	Without nonbreeders	With nonbreeders	Without nonbreeders
1988	No data	No data	1.58 (12) ^a	0.22 (9) ^a
1989	2.20 (5)	2.14 (7)	1.25 (8)	1.36 (14)
1990	1.89 (9)	1.00 (6)	0.25 (8)	0.15 (13)
1991	1.67 (6)	2.14 (7)	2.11 (9)	1.00 (12)
1992	1.75 (12)	1.75 (4)	1.17 (12)	0.42 (19)
1993	1.80 (10)	2.50 (4)	2.67 (15) ^b	1.31 (16) ^b
$\bar{x} \pm SD^b$	1.83 \pm 1.34	1.89 \pm 1.17	1.62 \pm 1.54	0.77 \pm 1.29

* Values with same superscript differ significantly ($P < 0.05$) between breeder classes.

^b Grand mean combining data across years.

f nonbreeders on Florida Scrub-Jay reproductive success of experienced pairs on John F. Kennedy Space Center, Florida. Values are $\bar{x} \pm SD$, with n in parentheses.*

	T4 site (1989-1993)		HC site (1988-1993)	
	With nonbreeders	Without nonbreeders	With nonbreeders	Without nonbreeders
	0.55 (28)	0.57 (11)	0.33 (55)	0.21 (72)
	1.92 ± 1.26 (26)	1.90 ± 1.29 (10)	1.85 ± 1.61 (40) ^a	1.08 ± 1.47 (51) ^a
	1.35 ± 1.26 (26)	0.70 ± 0.67 (10)	0.95 ± 1.16 (40) ^b	0.37 ± 0.69 (51) ^b
	0.69 ± 0.93 (26)	0.60 ± 0.70 (10)	0.60 ± 0.87 (40) ^c	0.25 ± 0.56 (51) ^c
survival	0.75 (44) ^d	0.37 (19) ^d	0.51 (74) ^a	0.34 (55) ^a
survival	0.58 (26)	0.86 (7)	0.63 (38)	0.68 (19)

npt differ significantly ($P < 0.05$) between breeder classes.

rease. Annual family sizes in typical for HC and Archbold years. Nonbreeders and usually indicative of past years (Woolfenden and Fitzpatrick 1984, Breininger et al. 1995). Trends were confounded at T4, where the number of produced was the same as the females lost to mortality. Nesting into T4 were tame, sug- gested from nearby sub- habitat loss and fire exclu- sion (Woolfenden and Fitzpatrick 1984, Breininger et al. 1995). Nonbreeders had no influence on repro- ductive success at T4 except for fledgling-to- juvenile survival. Pairs with nonbreeders at KSC had higher fledgling-to-juvenile survival. Non- breeders often enhance fledgling but not ju- venile survival at Archbold (Woolfenden and Fitzpatrick 1984, Mumme 1993). Pairs that in-

nale yearlings produced was half of the number of breed- ing at HC. Low HC fledgling

production, particularly for pairs without non- breeders, was responsible in large part for the population decline at HC. Low nesting success resulted from high nest predation, presumably by snakes, because few depredated nests showed signs of disturbance such as broken egg shells or altered nest structures (Woolfenden and Fitzpatrick 1984, Schaub et al. 1992). The low hab- itat suitability at HC, attributable to many tall shrubs and few openings among scrub oaks (Woolfenden and Fitzpatrick 1984, Breininger et al. 1995, Duncan et al. 1995), may have been responsible for higher predation on nests and female breeders, compared with the Archbold population.

Reproductive success was usually highest for pairs with nonbreeders at HC and Archbold (Woolfenden and Fitzpatrick 1984, Mumme 1993). Nonbreeders had no influence on repro- ductive success at T4 except for fledgling-to- juvenile survival. Pairs with nonbreeders at KSC had higher fledgling-to-juvenile survival. Non- breeders often enhance fledgling but not ju- venile survival at Archbold (Woolfenden and Fitzpatrick 1984, Mumme 1993). Pairs that in-

Florida Scrub-Jay breeders with and without nonbreeders at John F. Kennedy Space Center. Values are \bar{x} , with n in parentheses.*

	T4 site		HC site	
	With nonbreeders	Without nonbreeders	With nonbreeders	Without nonbreeders
No data	No data	No data	0.79 (24)	0.79 (19)
0.88 (8)	0.79 (14)	0.79 (14)	0.75 (16)	0.70 (30)
0.85 (13)	0.75 (12)	0.75 (12)	0.94 (16)	0.85 (26)
0.80 (10)	0.75 (16)	0.75 (16)	0.77 (22) ^a	1.00 (22) ^a
0.75 (24)	0.75 (8)	0.75 (8)	0.82 (28)	0.77 (43)
0.71 (14)	0.75 (8)	0.75 (8)	0.73 (30)	0.81 (32)
0.78 (69)	0.76 (58)	0.76 (58)	0.79 (136)	0.81 (172)

npt differ significantly ($P < 0.05$) between breeder classes.
ata across years.

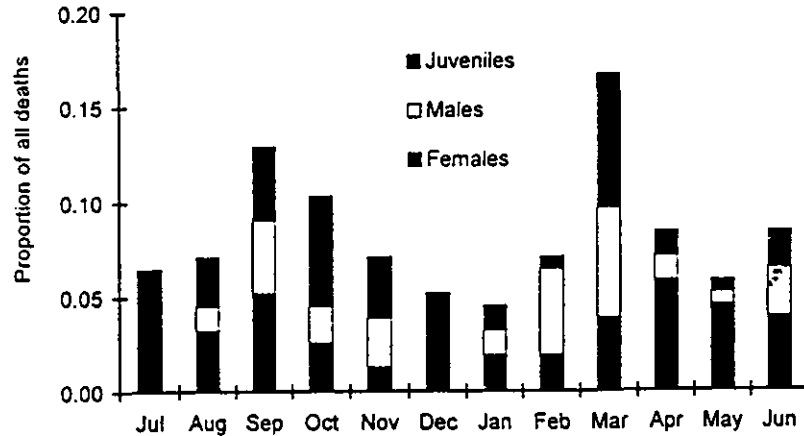


FIG. 2. Seasonal patterns of Florida Scrub-Jay mortality on John F. Kennedy Space Center.

cluded at least one novice breeder had lower reproductive success than pairs that had two experienced breeders at Archbold (Woolfenden and Fitzpatrick 1984) and HC, but not at T4.

The lack of a consistent influence of nonbreeders on breeder survival at KSC differed from Archbold, where pairs without nonbreeders died at 1.5 times the rate of pairs with nonbreeders (Woolfenden and Fitzpatrick 1984). Although Florida Scrub-Jay nonbreeders enhance predator detection (Woolfenden and Fitzpatrick 1984, McGowan and Woolfenden 1989), they also may attract hawks to nest sites and increase the frequency that breeders en-

gage in territorial disputes (Skutch 1961, Treisman 1975). Pairs with nonbreeders at HC tended to occur in areas with unusually small territory sizes and an abundance of scrub oaks and man-made openings. At Archbold, high nonbreeder densities have negative effects on survival of breeders in the entire study population (Woolfenden and Fitzpatrick 1984:fig. 9.11).

Few or no sex differences in breeder mortality occur at Archbold (Woolfenden and Fitzpatrick 1984), unlike KSC where breeder mortality appeared greater for females than males during nesting. Only females incubate and brood, possibly explaining their higher mortality rates

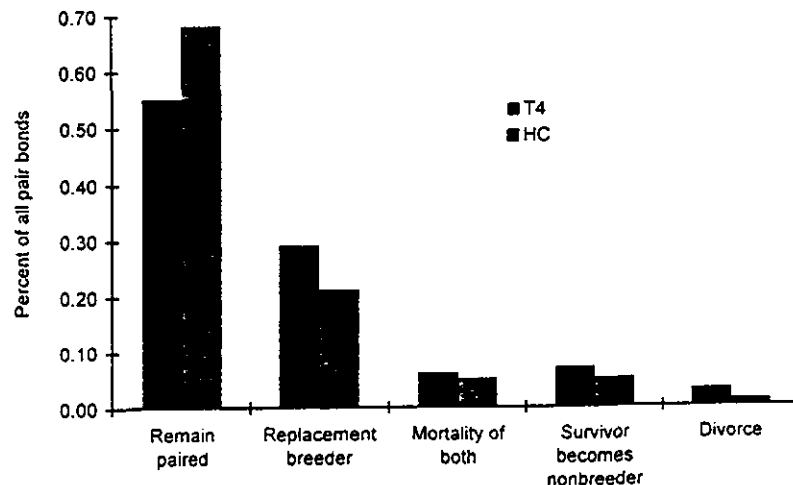


FIG. 3. Characteristics of pair bonds between successive breeding seasons: (1) breeders remained paired together between successive years; (2) survivor paired with replacement breeder following death of spouse; (3) both breeders died; (4) survivor became nonbreeder after losing territory and spouse to mortality; and (5) breeders divorced and paired with other breeders or became nonbreeders.

es in Florida Scrub-Jay breeder survival at John F. Kennedy Space Center. Values are
ses.*

T4 site		HC site	
Females	Males	Females	Males
No data	No data	0.77 (22)	0.81 (21)
0.83 (12)	0.83 (12)	0.70 (23)	0.74 (23)
0.69 (16)	0.80 (15)	0.76 (22) ^a	1.00 (21) ^a
0.79 (14)	0.79 (14)	0.82 (22)	0.95 (22)
0.69 (16)	0.75 (16)	0.74 (38)	0.85 (33)
0.64 (14)	0.79 (14)	0.74 (31)	0.81 (31)
0.72 (72)	0.79 (71)	0.75 (158)	0.85 (151)

ipt differ significantly ($P < 0.01$) between sexes.
ta across years.

s (as reported for other co-
Brown 1987, Koenig and
er's Hawks (*Accipiter coop-*
ned Hawks (*A. striatus*) of-
ds (Nelson 1968, Reynolds
ielefeldt et al. 1992, Joy et
en have been flushed from
ating that breeder females
edation while on the nest.
Cooper's Hawk was ob-
apparent Florida Scrub-Jay
containing many Florida
nd from which immediate-
eding female was missing.
female was found injured,
marks in the head, after
of a Cooper's Hawk flush-
wks are rarely seen in Arch-
; the jay nesting season
oolfenden 1989). Several
-shinned hawks were seen
SC scrub on nearly every
nd April. Nest defense calls
s often were given in re-
ce at HC, and young Coop-
asionally seen in HC scrub.
in winter at KSC and Arch-
sources were minimal (Brein-
nden and Fitzpatrick 1984).
r adults or nestlings (Wool-
ick 1984). Breeder mortality
old in June and July when
scrub and when snakes are
ors of juveniles and adults
tzpatrick 1984, Schaub et al.
eder and juvenile mortality
fall (Cruickshank 1980) and
tion (see above). Migrating
ficant mortality for other
al. 1984, Lindström 1989).

Archbold hawk sightings average fewer than
1.2 per h during the season of highest raptor
abundance (McGowan and Woolfenden 1989).
At KSC, 20 to 30 accipiter passes (accipiter flying
towards fleeing Florida Scrub-Jays) occasionally
have been observed within 30-min periods. Each
of these 30-min periods often involved at least
one Cooper's Hawk and several different Sharp-
shinned Hawks.

Patterns of delayed breeding, nonbreeder
distributions (except sex ratios), and pair-bond

TABLE 6. Fates of Florida Scrub-Jay nonbreeders be-
tween years at John F. Kennedy Space Center. Ta-
bled entries represent individuals.

Fate	T4 site		HC site	
	Females	Males	Females	Males
Juveniles to one-year olds*				
Die	9	1	9	4
Nonbreeders ^b	24	25	21	29
Novice breeders	1	1	4	1
One-year-olds to two-year-olds				
Disappear ^c	8	4	3	3
Nonbreeders ^b	7	11	6	10
Novice breeders	5	5	4	7
Two-year-olds to three-year-olds				
Disappear ^c	1	2	0	1
Nonbreeders ^b	3	4	0	8
Novice breeders	2	5	4	0
Three-year-olds to four-year-olds				
Disappear ^c	1	1	0	0
Nonbreeders ^b	0	2	0	2
Novice breeders	1	1	0	1

* Excluded 22 T4 juveniles and 9 HC juveniles that died before sex
determination. Juveniles were sexed as males if no hiccup calls were
heard by January. Because males make no hiccup calls, females could
be sexed before males. Thus, sex comparisons of juvenile survival should
not be performed.

^b These jays had delayed breeding and were potential helpers.

^c Older nonbreeder disappearances were mostly from mortality or
dispersal (where a few jays dispersed beyond our surveys).

fidelity were similar within periodically burned habitat at KSC and Archbold (Woolfenden and Fitzpatrick 1984). The male-to-female sex ratio of nonbreeders at Archbold (1.1 to 1.0) was similar to that at T4 (1.2 to 1.0), but much lower than at HC (2.2 to 1.0). First-year females were more likely to become novice breeders at HC than at T4 or Archbold (Table 6). Perhaps this was because there were more opportunities to breed at earlier ages at HC because of demographic trends. Other data (Breininger, Oddy, and Larson unpubl. data) in unburned scrub and urban areas showed poor reproductive success, small family sizes, and many male and female jays achieving breeder status at one year of age.

Nest predation explained differences between Florida Scrub-Jay demography in unburned and periodically burned scrub at Archbold (Woolfenden and Fitzpatrick 1984, 1991). The numbers, types, and seasonality of predators and habitat differences influencing the vulnerability of Florida Scrub-Jay nests, juveniles, and adults to predation may have accounted for some of the few differences in demography and delayed breeding between KSC and Archbold.

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